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**FEEDING TRACES OF RECENT RAY FISH AND ABUNDANT OCCURRENCES
OF THE TRACE FOSSIL *PISCICHNUS WAITEMATA* FROM THE PLIOCENE OF
SANTA MARIA ISLAND, AZORES (NORTHEAST ATLANTIC)**

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ABSTRACT: The bowl-shaped trace fossil *Piscichnus waitemata* Gregory, 1991 appears in Pliocene sandstones from Santa Maria Island (Azores Archipelago), extensively excavated during a stage of island evolution when the volcanic edifice was a guyot (flat-topped seamount) isolated in the NE Atlantic. The host sediments were deposited at depths from the intertidal zone to fair-weather wave base in a tropical climate, also under the influence of storms and hurricanes. The traces were produced by ray fishes hunting for polychaetes, crustaceans and bivalves living in the sediment, similar to present-day nearshore, warm waters in the Azores, Baja California Sur (Mexico), and New Zealand, from which examples of feeding depressions are drawn (incipient *Piscichnus*). While *P. waitemata* is abundantly present in planar sediments on top of the guyot, far fewer trace fossils occur in sandstone deposited on the guyot's margins. Presumably, the different densities of ray holes in the two sedimentary bodies was a response to a lesser availability of organisms preyed on by the ray fishes, a lower seawater temperature (due

to the greater depths), and a more dynamic environment in which life conditions were less favorable. Moreover, the potential preservation of bowl-shaped depressions was lower in this setting, given the steepness of the seafloor, stronger currents, and constant sediment mobility. Therefore, the top of the guyot was a more favorable habitat, refuge and/or nursery ground for many ray fishes. Measurement of the diameter of the ray holes resulted in three distinct size classes, suggesting that several species were responsible for their formation.

INTRODUCTION

Benthic fishes are known for their diverse tracemaking activity. Examples including resting traces (Seilacher 1953), large predation depressions (Gregory et al. 1979), deep, domichnial burrows (e.g., Stanley 1971; Able et al. 1987; Boyer et al. 1989; Atkinson and Taylor 1991) and shallow feeding depressions (Pearson et al. 2007; Muñiz et al. 2015) have been described from recent environments. Swimming trails, such as *Undichna* Anderson, 1976, and feeding traces (e.g., *Osculichnus* Demircan and Uchman 2010) occur starting in the Devonian (e.g., Trewin 2000; Gibert 2001; Soler-Gijón and Moratalla 2001; Szrek et al. 2016). Finally, bowl-shaped depressions made by fish when nesting or feeding are known as *Piscichnus* Feibel, 1987 (Gregory 1991) and have been reported with the earliest known occurrences from Upper Cretaceous strata (Howard et al. 1977).

Some ray fish species (Elasmobranchii: Batoidea) are predators, searching for food in sediments. They produce characteristic bowl-shaped depressions, which popularly are called ray holes, either by flapping their pectoral fins or by hydraulically blowing away sediment through their mouth. These depressions can be preserved in a fossil state and are distinguished as the trace fossil *Piscichnus waitemata* Gregory, 1991. Their abundance is variable, from

single findings to mass occurrences in some deposits (e.g., Gregory 1991; Martinell et al. 2001; Kotake and Nara 2002; Löwemark 2015). One of the richest occurrences of *Piscichnus* occurs in lower Pliocene sedimentary deposits on the NE-Atlantic island of Santa Maria (Azores Archipelago). Their high abundance, location on a volcanic oceanic island, and association with other trace fossils make these occurrences remarkable. Hence, the main aim of this paper concerns the description and interpretation of these “holes”. Moreover, recent traces of ray fishes in the Azores, Mexico’s Gulf of California, and New Zealand are presented here and their environmental context is discussed. Additionally, a review of the ichnogenus *Piscichnus* is provided.

Fossil traces left by ray fishes are a source of information and an important component of bioturbation structures. They are commonly overlooked, mistaken for physical sedimentary structures, or underestimated in palaeoenvironmental interpretations. In this contribution, we show their interesting aspects and value, and underline the link between paleo- and neoichnology, in which observations from a biological and geological perspective are integrated.

PLIOCENE DEPOSITS OF SANTA MARIA ISLAND

The evolutionary history of Santa Maria Island was described in detail by Ramalho et al. (2017), who unraveled a complex geological history, showing a subsidence rate of about 100 m/Ma from ~6 Ma up to circa 3.5 Ma, followed by a general uplift trend of about 60 m/Ma (probably as a result of crustal thickening by basal intrusions) until present time. Santa Maria is the oldest island in the Azores archipelago, the only one known to have emerged before or even during the Pliocene (Sibrant et al. 2015; Ramalho et al. 2017; and references

therein). The earliest stage of Santa Maria as an island emerged around 6 Ma ago as a result of
surtseyan activity that subsequently changed to subaerial activity, forming a shield volcano
ca. 5.8-5.3 Ma that corresponds to the Anjos Volcanic Complex. Between 5.3 and 4.1 Ma,
subsidence and marine erosion slowly dismantled the volcanic edifice, resulting in the nearly-
complete truncation of the first island of Santa Maria, to form a wide and shallow guyot-like
structure (a large and flat-topped seamount, called guyot for simplification). However, we
cannot exclude the persistence of a few residual surtseyan cones protruding above sea level
during this guyot phase, constituting more resilient or ephemeral rocky islets on top of the
shoal. Notwithstanding this possibility, erosion and sedimentation were predominant over
volcanism during this stage, as attested by the thick volcano-sedimentary sequence of the
Touril Volcano-sedimentary Complex, which increases in its marine character towards the
top. The second phase of island development on Santa Maria (the Pico Alto Volcanic
Complex) started ca. 4.1 Ma and lasted until ~3.5 Ma. Volcanism, then gradually changed
from large fissure-fed eruptions to smaller monogenetic eruptions and finally ceased at about
2.8 Ma (Ramalho et al. 2017).

As a result of a trend in uplift that started ca. 3.5 Ma (Ramalho et al. 2017), and due to
subsequent erosional processes, over 20 outcrops, most of them with Pliocene fossiliferous
sediments, are now available for study (for a review, see Ávila et al. 2016a, 2018). Among
them, the most important and well-studied Pliocene outcrops are: (1) Pedra-que-pica, an
exceptional shallow-water shell bed (coquina) with a bivalve-dominated fossil assemblage
that was deposited below fair-weather wave base, at around 50 m depth (Kirby et al. 2007;
Ávila et al. 2015a); (2) Ponta do Castelo, a sequence of fossiliferous tempestites that was
deposited at ~50 m depth, on a narrow and energetic insular shelf, as a result of massive
sediment remobilization from the nearshore to the middle/outer shelf (Meireles et al. 2013);
(3) An outcrop informally called the “Ichnofossil’s Cave”, a huge wave-cut notch exposure in

the sea cliff, with a bioclastic, fossiliferous sandstone layer very rich in trace fossils (Santos et al. 2015); and (4) Malbusca, a volcano-sedimentary sequence with accumulations of rhodoliths (unattached coralline red algae) capped by a massive sandstone bed, which was interpreted as an amalgamation of tempestites deposited under increasing water depths (Rebelo et al. 2016), probably as a result of hurricanes occurring during the Pliocene Warm Period, with El Niño conditions more intense than today (Johnson et al. 2017).

The Pliocene faunas from these outcrops comprise numerous species of a variety of higher taxa: brachiopods (Kroh et al. 2008), gastropods (Janssen et al. 2008; Ávila et al. 2016b), crustacean barnacles (Winkelmann et al. 2010), crustacean ostracods (Meireles et al. 2012), echinoids (Madeira et al. 2011; Santos et al. 2015), bryozoans (Ávila et al. 2015a; Rebelo et al. 2016), cetaceans (Estevens and Ávila 2007; Ávila et al. 2015b) and rhodolith-forming coralline algae (Rebelo et al. 2014). Ichnofossils are also abundant (Santos et al. 2015; Uchman et al. 2016, 2017; this work). Although the presence of selaceans during the Pliocene was reported by Ávila et al. (2012), on the basis of a small number of teeth found at these outcrops, the absence of evidence for batoids puzzled these authors.

PISCICHNUS IN PLIOCENE SEDIMENTS OF SANTA MARIA

The trace fossil *Piscichnus waitemata* from Santa Maria is exclusively observed in Pliocene sediments, foremost in sandstones up to 25 m thick from the Malbusca section that rest on the erosionally truncated Touril Volcano-sedimentary Complex. Although much less abundant, they can also be found in other (still Pliocene) sedimentary wedges sandwiched between volcanic rocks of this complex (Ichnofossil's Cave section, at a slightly lower

stratigraphic position), or at the top of this complex, underneath volcanic rocks of the Pico Alto Volcanic Complex (Ponta do Castelo section).

In the Malbusca section, numerous trace fossils of *Piscichnus waitemata* are observed mostly in horizontal but also in vertical and oblique cross sections, which perfectly show the characteristic bowl-shaped depressions filled with sediment (Figs. 2, 3). The trace fossils are slightly elliptical to circular in outline, with the longer axis of the ellipse or radius ranging from 5 to 45 cm in length. A plot of measurements shows three size groups: the smallest between 5 and 10 cm in length, the dominant group between 13 and 28 cm, and yet a third group ranging from 35 to 45 cm (Fig. 4). The size values should be treated with caution, however, because they depend also on the plane of intersection on which the traces are observed and should be considered as minimum values.

The outline of the depressions is mostly regular, sharp and smooth. The depressions are usually up to 15 cm, exceptionally up to 35 cm deep (Fig. 5). In cross section, the depression is mostly observed as a symmetrical arc with divergent limbs (Figs. 2D, 2F, 3A), rarely with subparallel limbs (only in the deepest forms), and more rarely it forms an asymmetrical sack-like depression. Almost exclusively, the width is greater than the depth. Only a few structures are deeper than wider, with a short, basal cylindrical extension, which is four to five times narrower than the main part of the burrow (Fig. 5). The margin of the depression is sharp and regular. Some of the depressions are crisp in outline and well visible, whereas others are visible only under special conditions of light and rock moisture. Some of them are preferentially eroded and they form shallow cavities in the exposure (Fig. 3C, 3D, 3E, 3F). Therefore, the real density of the burrows is probably underestimated. The noticeable abundance varies from place to place and can attain a few depressions/m². Usually, they are spaced a few or several tens of centimeters apart in areas with the highest densities. Some depressions can overlap (Fig. 2B, 2B), while the size and filling of the overlapping

depressions can be different. Rarely, the depressions can be seen as serially arranged (Fig. 3B).

The depressions are filled by sandstone which is similar overall to the surrounding rock, from which it differs in color hue, ichnofabric and minor structural/textural features. However, the grainsize of the filling is usually distinctly coarser (coarse to very coarse sands with interspersed pebbles and bioclasts), occasionally including whole rhodoliths; Figs. 2D, 2E, 2F, 3A). The coarsest grains and largest bioclasts are present in the lowest part and on one side only. In fine-grained sand, the filling is massive and bioturbated. The most common co-occurring trace fossil is *Macaronichnus segregatis* Clifton and Thompson, 1978, the abundance and visibility of which can be different in the filling and the surrounding sediments (Figs. 2A, 2B, 2CC, 5). In some fillings, the trace fossils *Thalassinoides* isp. and *Ophiomorpha nodosa* Lundgren, 1891 are present (Figs. 2A, 2B, 2C, 5A) but some depressions may truncate *Thalassinoides* isp. (Fig. 2C). Rarely, *Palaeophycus* isp. is present in the depressions, usually together with *Macaronichnus* (Fig. 2C). The depressions can cross through layers riddled with the irregular echinoid burrow *Bichordites monastiriensis* Plaziat and Mahmoudi, 1988, and enter a layer reworked with *Macaronichnus segregatis* (Fig. 3E, 3F). Most of the *Piscichnus* depressions are present in totally bioturbated sediment. More rarely they cross cut horizontally laminated sandstones (Fig. 5B), some of which contain the trace fossil *Dactyloidites otto* (Geinitz 1849).

OCCURRENCES OF RAY FISHES AND THEIR TRACES IN THE AZORES ARCHIPELAGO

Walbaum (1792) was the first author to publish a scientific article applying the principles of binomial nomenclature and reporting elasmobranchs from the Azores [the Myliobatidae *Mobula mobular* (Bonnaterre 1788)]. Almost a century later, Hilgendorf (1888) reported five shark and four ray species. The list for elasmobranchs in the Azores was, among many others, further increased by Ferreira (1939), a local priest, who reported 18 shark and seven ray species. More recently, Barreiros and Gadig (2011) listed 37 shark and 13 batoid species for the region, although many are migratory and were only occasionally sighted. Lastly, Das and Afonso (2017) updated the annotated checklist for elasmobranchs, adding two shark and four ray species. Regarding batoids, only a few species are of significant economic relevance for the Azoreans, particularly some stingrays (order Myliobatiformes Compagno 1973), which, according to direct *in situ* observations, seem to be the producer of most ray holes observed nowadays in the archipelago. The common stingray *Dasyatis pastinaca* (Linnaeus 1758) and the common eagle-ray *Myliobatis aquila* (Linnaeus, 1758) are the most abundant stingrays in Azorean waters (Barreiros and Gadig 2011). However, the following species of stingrays also occur in the Azores: *Dasyatis cf. centroura* (Mitchill 1815), *Pteroplatytrygon violacea* (Bonaparte 1832) and *Taeniurops grabata* (Geoffroy Saint-Hilaire 1817). None are actively sought by local fisheries or have any commercial value as food. Their economic importance, however, is increasing with greater interest in recreational SCUBA diving and underwater photography.

Dasyatis pastinaca inhabits rocky and sandy bottoms down to 200 m depth and exhibits an angular and slightly short snout, with a rhomboid disk with an almost straight anterior margin of pectoral fins averaging 60 cm in disc width (Whitehead et al. 1984; Yeldan et al. 2009). This species can be found in the East Atlantic from southern Norway to South Africa, including the Azores, Madeira and Canary Islands (Barreiros and Gadig 2011; Yigin and Ismen 2012). *Myliobatis aquila*, which has a head clearly detached from the pectoral fins

that are wide and angled, can be found in shallow waters, bays and estuaries (Compagno 1986), as well as in offshore waters down to 537 m (Whitehead et al. 1984). With a disk width up to 1.5 m, this species occurs in the NE Atlantic, from the British Islands to Morocco and South Africa, in the Mediterranean (Capapé et al. 2007; Barreiros and Gadig 2011) and in the Macaronesian archipelagos of Madeira and the Azores (Whitehead et al. 1984; Patzner et al. 1992; Debelius 1997; Santos et al. 1997; Harmelin-Vivien et al. 2001; Saldanha 2003; Barreiros and Gadig 2011). Both species are also known to form aggregations for feeding, reproduction and spawning (Garcia 2008; Semeniuk and Rotley 2008; Barreiros and Gadig 2011; Afonso and Vasco-Rodrigues 2015; P. Torres, personal observations, 2016), which can be observed in the Azores in some areas, e.g., in Madalena Islets (Pico Island), Mosteiros Islets (São Miguel Island), Cabras Islets (Terceira Island), Castelete (Lajes do Pico, Pico Island), and Monte da Guia (Faial Island), attracting recreational SCUBA divers who come to observe.

Dasyatis pastinaca and *Myliobatis aquila* are common coastal species associated with sandy, muddy and rocky bottoms, occupying surface waters to depths of over 200 m (Fig. 6A, 6B). In the Azores, and according to Ponte et al. (2016), the diet of *D. pastinaca* consists mainly of decapod crustaceans (81% IRI – Index of Relative Importance) while *M. aquila* feeds mainly on mollusks (82% IRI), nonetheless both smash carapaces and shells of small crustaceans and mollusks. After having detected their endobenthonic prey, the rays excavate it by flapping their pectoral fins and/or by taking in water through the spiracles on top of the head and blowing water through their mouth, eroding the substrate hydraulically to produce a hole underneath them. The holes are subsequently refilled with new sediment (see video in Supplemental Material). The biogenic sedimentary structures that result from this activity are composed of two parts: a broad, shallow, surface depression that is dish-shaped, between 10 and 100 cm in diameter, and a lower, roughly circular depression that is as much as 15 cm

deep, depending on species and size (Fig. 6C, 6D). The excavated sediment accumulates near the posterior end of the ray, resulting in a certain asymmetry with a steeper slope at one end of the hole. Often, it is possible to observe shell detritus in the center (Fig. 7), which results mostly from the crushing and rejection of the shells after preying on bivalves. The depth of the hole and height of the adjacent ridge is dependent on how recently the depression was formed in relation to wave and current action, which are particularly effective in sandy sediments, and may thus disappear in a couple of days. These depressions produced by rays are quite common in the sandy bottoms that surround the islands, distributed widely throughout the middle and lower intertidal zones and even at greater depths (20 m).

OTHER EXAMPLES OF RECENT RAY HOLES

The recent feeding burrows of rays have been recognised by a number of biologists and geologists. Most are simple depressions, which are subcircular or elliptical in outline (Whitley 1940; Frey and Howard 1969; Cook 1971; Warne 1971; Howard and Frey 1975; Howard et al. 1977; Gregory et al. 1979; Gregory 1991; Myrick and Flessa 1996; Martinell et al. 2001) although lengthy trenches also have been reported (MacGinitie 1935). Bigelow and Schroeder (1953) noted the significance of feeding holes made by rays from Australia, and Whitley (1940) published a photograph of these structures from a low-tide beach at North Queensland, Australia. Nichols (1965) mentioned them from the Sonoran Coast of Mexico, MacGinitie and MacGinitie (1968) discussed trenches excavated by rays in the California coast, and Warne (1971) also mentioned these structures at Mugu Lagoon in California.

Cook (1971) reported depressions made by skates in the Connecticut coast while on Georgia, ray structures were discussed and illustrated by Frey and Howard (1969) from tidal

creek point bars, and Mayou and Howard (1969) mentioned them as characteristic biogenic features useful in distinguishing fluvial from estuarine point bars. Five species of rays and two skates occur in Georgia (Dahlberg and Heard 1969; Dahlberg 1972), while the southern stingray *Hypanus americanus* (Hildebrand and Schroeder 1928) (= *Dasyatis americana*), the bluntnose stingray *Hypanus say* (Lesueur 1817) (= *Dasyatis say*) and the Atlantic stingray *Hypanus sabinus* (Lesueur 1824) (= *Dasyatis sabina*) are the producers of most excavations (Howard et al. 1977). The stingray *Dasyatis centroura* occurs in offshore shelf waters and the cownose ray *Rhinoptera bonasus*, excavates shallow trenches in the bottom sediments when feeding on bivalves (Bigelow and Schroeder 1953). Between April and October, thousands of ray holes can be observed at low tide by aerial reconnaissance along the Georgia coast. On the surface of intertidal areas, ray feeding depressions can be observed and usually vary from 6 cm to as much as 1 m in diameter (Howard et al. 1977).

Several different ray species thrive in the subtropical waters of Mexico's Gulf of California, also known as the Sea of Cortéz. One of the more abundant is the round stingray, *Urobatis halleri* (Cooper 1863). It is relatively small with a characteristically broad, flat body shape and the extension of a short tail armed with a long, serrated stinging spine. Ray holes attributed to this species were observed as depressions in carbonate sand exposed during the receding tide off a small pocket beach on Isla Coronados (Fig. 8A, 8B). The animals that produced the holes were still actively swimming in the shallow waters nearby when the beach was photographed. The sandy substrate consists of fine-grained carbonates derived from crushed rhodoliths washed ashore from the shallow, subtidal zone where the algae are abundant. Flexible tubes that line the living space of marine polychaetes are visible protruding from the sand (Fig. 8A), and it is assumed that the rays were feeding on the polychaetes. The ray-hole impressions are unusual, because they capture details of both the head region and the tail (Fig. 8B). The average head width so recorded is 35 cm across and the average tail length

is about 40 cm. Feeding behavior, in this case, was gregarious based on the cluster of ray holes and the number of rays still swimming close by.

Farther north within Bahía Concepción at El Requesón, daily tides flood and re-expose a 350-m long tombolo that connects Isla Requesón with the peninsular mainland. The tombolo sand is dominated by the coarse debris of rhodoliths crushed by storm waves. The local name for this place (El Requesón) is a reference to “cottage cheese” the texture of which superficially looks much like that of sun-bleached rhodoliths. During high tide, round sting rays commonly frequent the flooded tombolo in search of infaunal bivalves that are especially abundant along this part of the coast. Due to the coarseness of the tombolo sand, however, the ray holes left as a result of their excavations are poorly defined with nowhere near the degree of detail showing body shape as molded in the more fine-grained carbonate sand on Isla Coronados. However, the same communal feeding behavior by multiple rays has been observed both at Isla Coronados and El Requesón.

On the tidal flat of Estero Morua, near Puerto Peñasco (Sonora, western Mexico), stingray traces are also commonly produced by the round stingray *Urobatis halleri* (Cooper 1863), showing circular to ovate depressions, between 10 and 30 cm in diameter with a gently sloped concave bottom 2 to 10 cm deep (Martinell et al. 2001). Less commonly, larger traces (up to 1 m diameter) with similar morphologic features are probably produced by the much larger diamond stingray *Hypanus dipterurus* (Jordan and Gilbert 1880) (= *Dasyatis dipterura*). The density of these traces varies, reaching up to 2 to 3 holes/m² and higher densities are found where food resources are more abundant.

Gregory et al. (1979) showed numerous ray feeding depressions on the broad intertidal and shallow subtidal sand and muddy sand flats of the Northern Island in New Zealand, which were made by the eagle ray *Myliobatis tenuicaudatus* Hector, 1877. Feeding depressions of eagle rays have been frequently seen on sandy substrates in water depths of up to 30 m near

the Poor Knights Islands off northern New Zealand (Gregory et al. 1979). In this area, they were observed by one of the authors of the present paper (A.U.) on the tidal flat of the Whatangau Estuary during a conference excursion (Gregory and Campbell 2005). Abundant depressions can be seen on the sandy flat during low tide, where the rays feed mostly on the bivalve *Macomona liliana* (Iredale 1915) (Fig. 8C). Well-preserved depressions show the body imprint of the ray and a circular pit in the anterior part of the body impression (Fig. 8D). The pits are 20–30 cm in diameter and up to 20 cm deep. In many depressions, excreted, crushed shells of the bivalve can be seen (Fig. 8E). The type material of the trace fossil *Piscichnus waitemata* Gregory, 1991 (specimen GR R09/717425 in the Palaeontology Collection, Geology Department, University of Auckland) is compared to the pits in feeding depressions of this ray. This ichnospecies is present in the type locality in the same region (Mathesons Bay), in Miocene sandstones of the Cape Rodney Formation, Waitemata Group (Fig. 8F).

DISCUSSION

The Ichnogenus Piscichnus and Recognition of Ichnospecies

Originally, *Piscichnus* was distinguished by Feibel (1987) in the lower part of the Pliocene Kobi Fora Formation in northern Kenya, where its type ichnospecies *P. browni* Feibel, 1987 occurs in lacustrine sandstones. It was interpreted as a nest of fishes and is characterized as a large and shallow bowl-like depression, 45–135 cm in diameter and 5–15 cm deep.

Later, Gregory (1991) distinguished *Piscichnus waitemata* in Miocene strata of New Zealand (see also Fig. 8F) and compared it to the recent feeding trace of *Myliobatis tenuicaudatus* (see also Fig. 8C, 8D, 8E) introduced earlier by Gregory et al. (1979). *Piscichnus waitemata* is diagnosed as “A steep-sided, cylindrical or plug-like to shallow, circular, dish-shaped structure of moderate to large size oriented concave upward, more or less vertical to bedding” (Gregory 1991). Its morphology and size agrees very well with *Piscichnus* observed in the Pliocene sediments of Santa Maria.

Burrows at the type locality of *P. waitemata* are mostly 15–20 cm, maximum 30 cm in diameter, and mostly up to 15 cm deep, with a maximum of 50 cm. Other data from the literature on the diameter of this ichnospecies are as follow: 10–15 cm (Schindler et al. 2005), 5–56 cm (Kotake 2007), up to 24 cm (Massari and D’Alessandro 2010), 10–30 cm (Löwemark 2015). Hence, the size of the depressions from Santa Maria fits these data very well. It is not excluded that the three size groups registered (cf. Fig. 4) reflect different taxa of the producers or different size/ages of individuals of the same species.

Belvedere et al. (2011) described irregular, non-overlapping depressions with radial elements ascribed to *Piscichnus*, but considered as the responsible producer, not rays, but the sturgeon (family Acipenseridae) as described by Pearson et al. (2007). Not only fishes but several animals can produce bowl-shaped feeding depressions in the sea floor, including the walrus, grey whale, or dolphins, and, in the intertidal zone, also the raccoon and grizzly bear (see Gingras et al. 2007, for a review), or shelduck (Cadée 1990). However, because of their different size and shape (and context), none of the depressions produced by the aforementioned animals match with the Pliocene traces from Santa Maria Island.

The earliest record of *Piscichnus* dates from the Late Cretaceous (Howard et al. 1977). Moreover, Soler-Gijon and Lopez-Martinez (1997) recovered abundant fossil ray teeth in coeval samples from the lower part of the Tremp Group in the Tremp Basin (Spain),

representing three fossil ray species: *Rhinobatos* sp., *Igdabatis indicus* Prasad and Cappetta, 1993 and *Rhombodus* sp. Species of the genus *Rhinobatos* (Family Rhinobatidae) are known bottom-feeders, and are still living today in shallow-water environments (Du Preez et al. 1990). Although the genus *Igdabatis* is known only from the Upper Cretaceous, the living relatives of the genus *Myliobatis*, a common producer of *P. waitemata*, is considered to have evolved from this clade (Soler-Gijón and Lopez-Martinez 1997). Thus, the first findings of body fossils of modern, bottom-feeding ray taxa correspond with the first occurrence of *P. waitemata*, suggesting that their morphology and behavior coevolved. Nevertheless, even older *Piscichnus* is possible, because the earliest batomorphs (skates and rays) are known since the Early Jurassic (Rasmussen and Arnason 1999).

Relation to Other Trace Fossils and Some Morphological Features

Piscichnus waitemata from Santa Maria Island is associated with other trace fossils (Fig. 9A), foremost *Macaronichnus segregatis*, produced by polychaetes leaving vertically oriented traces (Uchman et al. 2016), and with the crustacean burrows *Thalassinoides* sp. and *Ophiomorpha nodosa*. In some fillings of *P. waitemata*, *Macaronichnus* is more abundant than in the surrounding sediments. For a similar situation in Japan, Kotake (2007) suggested that this is related to deeper burrowing of the *Macaronichnus* tracemaker in the well mixed and oxygenated filling than in the surrounding area. This factor may have resulted in a better preservation potential of *Macaronichnus* in deeper tiers. Such situations, however, are not consistently found in Santa Maria, and in some ray holes *Macaronichnus* is less abundant than in the surrounding strata. Such contrasting situations are shown in two overlapping ray holes in Figure 2C. Probably, the nutritional value of the filling was the most important factor.

Piscichnus cross cuts crustacean burrows and is, in turn, cross cut by them (Figs. 2A, 2C, 5B). This proves contemporaneous burrowing of their producers. It is quite possible that the ray fish producer fed on the crustaceans, as suggested by spatial relations between *Ophiomorpha* and *Piscichnus* in the Miocene of Taiwan (Löwemark 2015). Also, polychaetes and bivalves or even fishes were probably the hunted target. Serial arrangement of *Piscichnus* (Fig. 3B) can be the result of feeding by the same animal along a confined path. This is typical behavior for stingrays when feeding upon shallow infaunal animals. This feeding behavior is the reason for the absence of overlapping traces as the animals try to avoid searching for food more than once in the very same place. As such, these holes are typically found in groups of similar size, locally aligned in a single row, likely resulting from a single ray foraging for food within a small area (Howard et al. 1977; Martinell et al. 2001).

The narrower basal extensions of *Piscichnus* (Fig. 5) could have resulted after the removal of bivalves or fish from their burrows after their exposure on the bottom of the depression. The partly crushed shells (Fig. 2D, 2E, 2F) may derive to some extent from the feeding, not necessarily from filling by currents. The differentiation of the filling texture may result also from sorting during the “blow job”, with the larger, heavier particles staying within the ray hole while only the finer ones are blown away. According to some authors, the depression left by ray fish is filled during or immediately after feeding (Kotake et al. 2004). However, numerous observations of recent depressions, including these from the Azores (see below), suggest that they are filled within some days. Such depressions are good traps for any kind of materials transported by current action, including the shells previously crushed by the feeding rays. The bioturbation rate by rays is very effective. Myrick and Flessa (1996) calculated that they can totally rework intertidal sediment within 72 days based in an observation site in the Gulf of California. The biological crushing and sorting should be taken

into account in consideration of distribution of skeletal material, which is not necessarily influenced by physical forces only.

Crossing of levels with *Bichordites* by *Piscichnus*, judging from the size in the middle–upper part of the latter (Figs. 3E, 3F, 9A), it is shown that *Bichordites*, a burrow produced by irregular echinoids, was tunneled not much more than 10 cm below the sea floor. This is consistent with observations on the modern analogue of the *Bichordites* tracemaker, i.e., *Echinocardium mediterraneum* (Forbes 1844), which burrows at the depth of 2–4 cm below the sea floor (Bromley et al. 1995). Another trace maker analogue, *Echinocardium cordatum* (Pennant, 1777), can burrow at a depth of 15–20 cm below the sea floor (Nichols 1959), though shallower (3–5 cm) in other places (Bromley et al. 1995), or even feed on the sea floor surface (Bromley and Asgaard 1975).

How Ray Fishes Dig Depressions

Skates and rays primarily feed in or on the bottom by biting pieces of sessile invertebrates or excavating buried prey, although some also feed in the water column. Rays uncover prey by pectoral “wing-flapping” and/or hydraulic mining by jetting water through the mouth (VanBlaricom 1976; Howard et al. 1977; Gregory et al. 1979; Muto et al. 2001; Carrier et al. 2012) although it is also acknowledged that rays expose buried mollusks by digging with their snouts (see Wheeler 1969). Excavation of benthic prey by rhythmic flapping of the rostrum and pectoral fins is also common amongst several rays, while the cownose ray *Rhinoptera bonasus* (Mitchill 1815) uses a combination of wing-flapping/water-jetting (Schwartz 1967, 1989; Sasko et al. 2006), and by production of under-pressure by body bending (Motta 2004).

Excavations made by the feeding activity of rays are commonly exposed in tidal flats and in estuarine sand bars and channels of the Georgia coast during low tide (Howard et al. 1977). In this region, Bigelow and Schroeder (1953) stated that rays "excavate the substrate with their pectoral fins" and MacGinitie and MacGinitie (1968) indicated that the ray "digs by flapping its 'wings', thus creating a current that causes the sand and mud to stream out behind it." Hence, in this case, the rays utilize external currents in the environment, given that their excavations are always oriented with the direction of current flow as determined from associated ripple marks.

During feeding, the eagle ray *Myliobatis tenuicaudatus* arches its wing tips, raising the forward part of the body and mouth above the bottom, jetting water with considerable force into the substrate. This behavior is known as "head bobbing" (cyclical cranial elevation and depression) and was already observed in captivity for *Rhinoptera bonasus* (Sasko et al. 2006). These head movements enhance buccal oscillation and flush fluidized sediment from feeding pits. Myliobatid and rhinopterid rays show an increase in the mass of the epaxial muscle when compared to other myliobatiform rays, which is used to lift the head (González-Isáis and Domínguez 2004).

Peculiarity of *Piscichnus* from Pliocene Sediments of Santa Maria

The occurrences of *Piscichnus waitemata* in Pliocene strata of Santa Maria Island represent one of the richest associations from the geological record. This may have been caused by the peculiar palaeoenvironmental conditions on Santa Maria at that time, and by the general, oceanographic location of the island. From 5.3 to 4.1 Ma, after erosion of the Anjos Volcanic Complex, the island became a wide and shallow, flat-topped seamount (or bank)

473 similar to a guyot, probably only with small islets emerging above sea level (Fig. 9B). Santa
 474 Maria's volcanic edifice thus constituted one of the few shallow-water environments in the
 475 whole of the NE Atlantic during the Pliocene. Sandy, fossiliferous, transgressive sediments
 476 accumulated at the top of this guyot in a tropical setting (see Ávila et al. 2016b). As
 477 demonstrated by a combination of sedimentological data on rhodoliths (Rebelo et al. 2014,
 478 2016), a massive hurricane bed (Johnson et al. 2017) and trace fossils (Uchman et al. 2016,
 479 2017), Pliocene sediments were deposited near the fair-weather wave base in the middle and
 480 inner insular platform sections of the guyot (Malbusca section), and under a less clear
 481 situation in the basal part of sandstone wedges (clinoforms), in which the main part with
 482 distinct foresets was deposited below the storm wave-base level in the vicinity of the edge of
 483 the insular platform located in the outer section of the guyot (Ponta do Castelo and
 484 Ichnofossil's Cave section). In both these cases, deposition took place under the influence of
 485 storms and hurricanes, especially in the marginal parts of the seamount. According to the
 486 literature (e.g., Howard et al. 1977; Gregory 1991; Schindler et al. 2005; Kotake 2007;
 487 Löwemark 2015), *P. waitemata* occurs elsewhere in comparable energy/bathymetric zones,
 488 usually in the *Skolithos* and the *Cruziana* ichnofacies, which ranges from the foreshore to
 489 upper offshore (e.g., Pemberton et al. 1991). Moreover, it can be expected that the
 490 temperature (a major driver of ray species' distribution and movement) of the shallow waters
 491 on the top of the guyot was higher than in the surrounding, deeper waters. Energetic demands
 492 of key metabolic and physiological processes (e.g., digestion, osmoregulation) are known to
 493 fluctuate in response to changes in abiotic factors, mainly temperature and/or salinity. In fact,
 494 many ray species are known to use diel movements to behaviorally thermoregulate, moving
 495 through the habitat in such a way as to maximize time spent at temperatures favorable for the
 496 joint conduct of its life processes (Matern et al. 2000; Schlaff et al. 2014). The bottom
 497 sediment was inhabited by abundant polychaetes, crustaceans and bivalves, which are the

typical prey of rays, as attested by the rich marine fossiliferous content of Santa Maria's Pliocene sediments (Ávila et al. 2015a, 2018).

Piscichnus waitemata is much less frequent in sediment wedges sandwiched between volcanic sequences, usually lava deltas located on the edges of the insular platform (Fig. 9B). So far, they have been found only in the Ponta do Castelo and Ichnofossil's Cave sections representing such settings. This distribution may have been caused by the presence of a more dynamic environment in such settings, with stronger influence of storms and hurricanes as well as frequent depositional/erosional events, and by the fact that such depositional areas were much steeper and relatively limited in size. Ecological conditions in such places were less favorable than on the middle/inner sections of the guyot/bank. Moreover, both the density of prey animals supporting the ray population as well as the preservation potential of feeding depressions were probably smaller under such conditions. Therefore, the flat top of the guyot was an ideal habitat, refuge, feeding and/or nursery ground for ray fish species.

CONCLUSIONS

Pliocene oceanic island sediments deposited at the top of shallow seamount contain abundant trace fossil *Piscichnus waitemata* (three size classes) produced by ray fishes feeding mostly on bivalves, crustaceans and polychaetes. They are much less frequent in small sedimentary wedges deposited on the flanks of the seamount than in the middle and inner insular platform sections of the guyot. The difference was likely influenced mostly by less favorable ecological conditions in the flanks and lower preservational potential than in calmer and shallower (intertidal zone to fair-weather wave base) environment at the top of the seamount.

Recent ray holes in the Azores are produced subtidally by a few, mostly non-migratory species.

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SUPPLEMENTAL MATERIAL

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Data are available from the PALAIOS Data Archive:

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875

FIGURE CAPTIONS

FIG. 1.—Maps of the Azores and Santa Maria, and general stratigraphical column. **A)** Location of the Azores within the NE Atlantic. **B)** Location of Santa Maria within the Azores Archipelago; bathymetry extracted from GEBCO_2014 Grid. **C)** Geological map of Santa Maria and respective legend, after Serralheiro et al. 1987 and Ramalho et al. 2017; studied sections marked with red rectangles. **D)** Position of studied sequence within the general volcano-stratigraphical column of Santa Maria, after Serralheiro et al. 1987 and Ramalho et al. 2017.

FIG. 2.—*Piscichnus waitemata* (*Pi*) in Pliocene sandy sediments of Santa Maria guyot (Azores), in the Malbusca (A–C, E, F) and Ichnofossil's Cave (D) sections. *Piscichnus* is visible in horizontal (A–E) and subvertical (F) sections in fine-grained (A–C) or coarse (D) sandstones. **A)** Numerous burrows of different size and visibility cross cut by *Thalassinoides* isp. (*Th*). **B)** A few, partly overlapped burrows cross cut by *Ophiomorpha* isp. (*Oph*). **C.** Two partly overlapping *Piscichnus*; the older one (left) is filled with sand showing abundant *Macaronichnus* (*Ma*) and the presence of *Palaeophycus* isp. (*Pa*), the younger one (right) cross cuts *Thalassinoides* isp (*Th*); both are cross cut by *Ophiomorpha* isp. (*Oph*). **D)** *Piscichnus* filled with very coarse pebbly sandstone rich in crushed mollusk shells. **E)** *Piscichnus* with bioclastic coarse filling rich mostly in bivalve shell valves and rhodoliths. **F)** *Piscichnus* with bioclastic coarse filling in the lower part.

FIG. 3.—*Piscichnus waitemata* (*Pi*) in Pliocene sandy sediments of Santa Maria guyot (Azores), in the Ponta do Castelo (A) and Malbusca (B–F) sections. **A)** Poorly visible *Piscichnus* in medium-coarse sand visible in vertical section and filled with coarse sand;

lower boundary marked by dashed yellow line. **B)** Series of burrows on subhorizontal surface of fine-grained, bioturbated sandstone. **C)** Numerous *Piscichnus* visible from below on an overhang oblique surface in bioturbated, fine-grained sandstone above a 5 m-thick storm bed (“big bed”; cf. Johnson et al., 2017). **D)** Numerous *Piscichnus* visible on an overhang oblique surface in bioturbated, fine-grained sandstone below a 5 m-thick storm bed (“big bed”). **E)** *Piscichnus* on lower bedding surface with abundant *Bichordites* (*Bi*). **F)** *Piscichnus* crossing a bed with abundant *Bichordites* (*Bi*) down to sandstone bioturbated with *Macaronichnus segregatis* (*Ma*).

FIG. 4.—Measurements of *Piscichnus* ray holes from Pliocene sediments of Santa Maria guyot (Azores).

FIG. 5.—Deep *Piscichnus* with an extension in the lowest part. Malbusca section; vertical surfaces. **A).** An example with abundant, commonly vertical *Macaronichnus segregatis* (*Ma*) and *Thalassinoides* isp. (*Th*). **B)** *Piscichnus* crossing horizontally laminated bed; abundant *Macaronichnus segregatis* (*Ma*) in the filling and the surrounding.

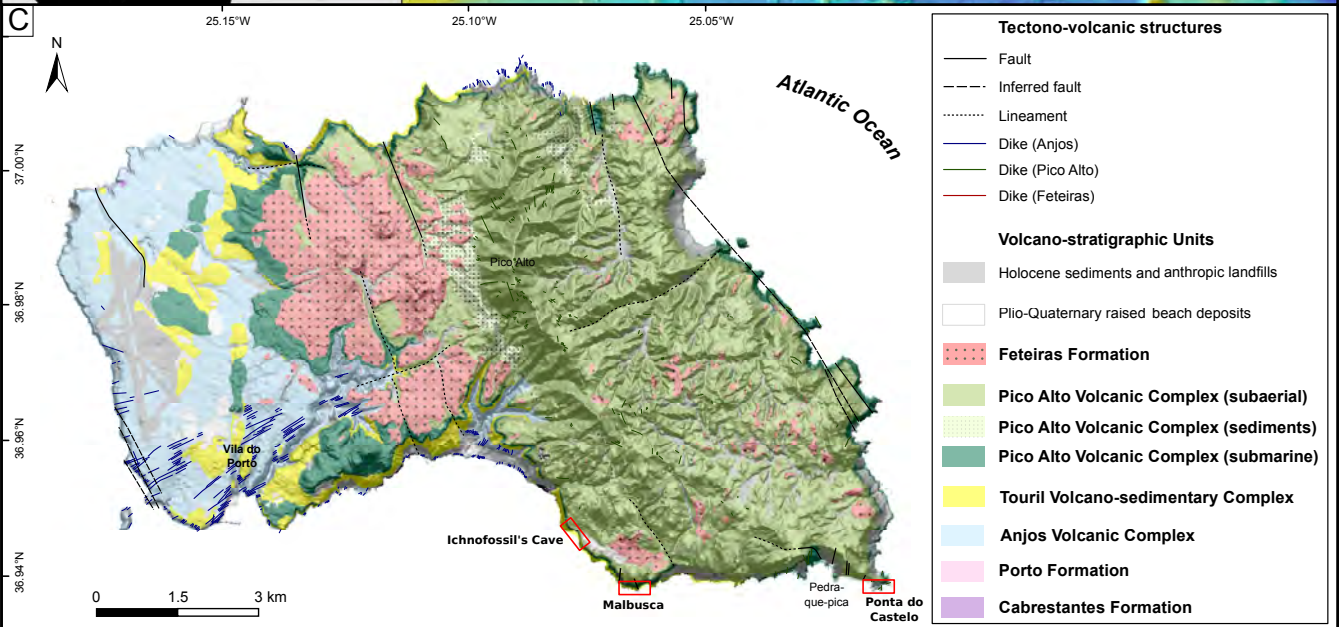
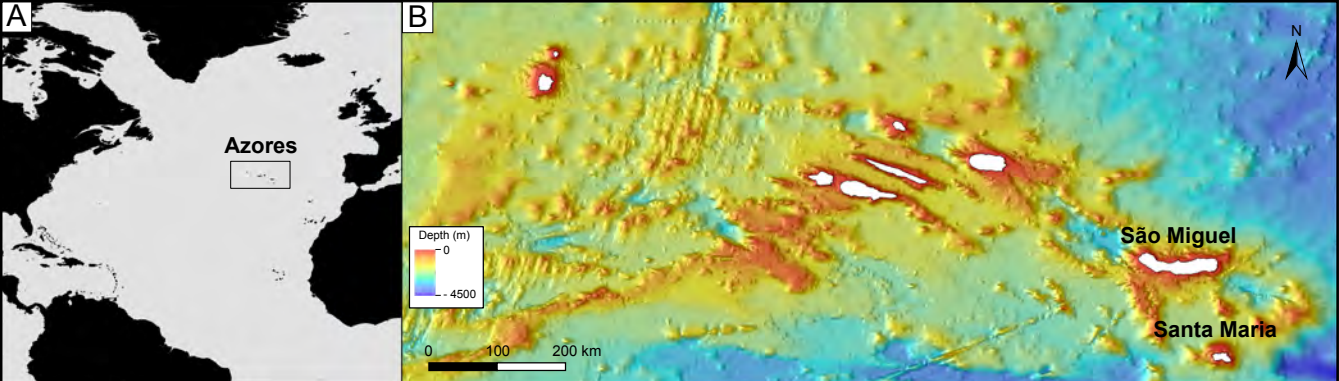
FIG. 6.—Modern ray holes (incipient *Piscichnus*) on the sea floor off the southern coast of São Miguel Island (Azores), at 12 m of water depth. Photographs by Gui Pinto da Costa. **A,** **B)** Stingray *Dasyatis pastinaca* lying on the bottom. **C, D)** Ray holes (rh) on the rippled sea floor.

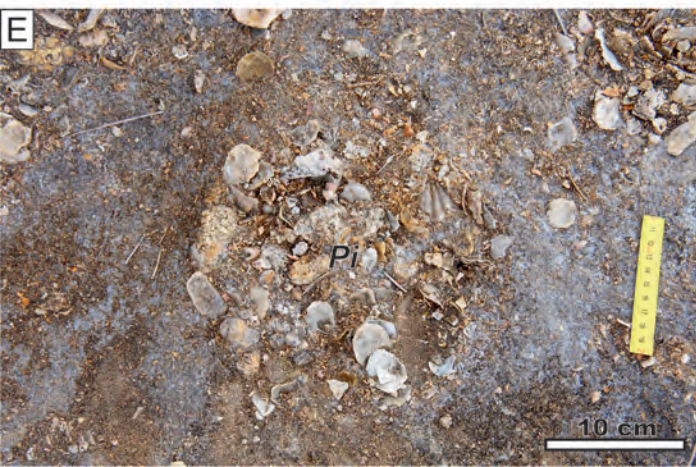
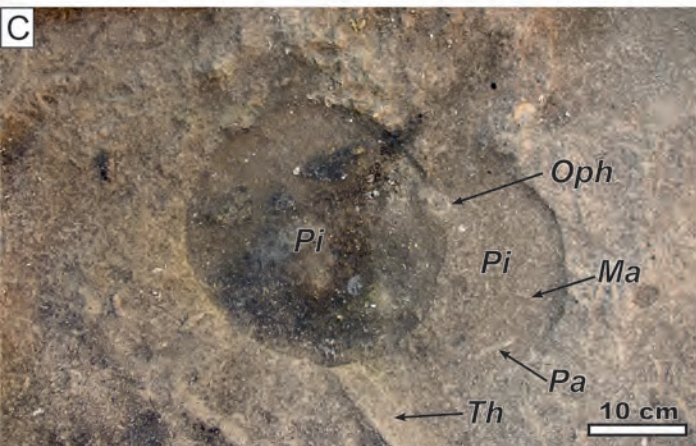
FIG. 7.—A modern ray hole (incipient *Piscichnus*) on the rippled sea floor off the southern coast of São Miguel Island (Azores), at 12 m of water depth. Photographs by Gui Pinto da

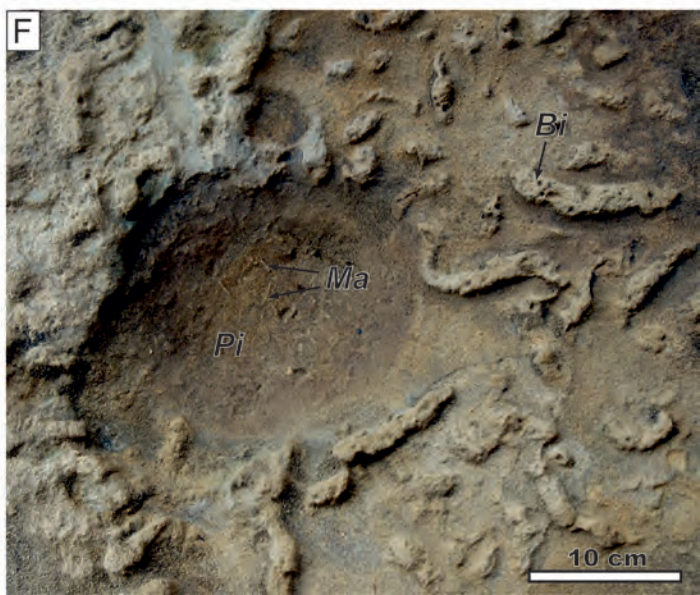
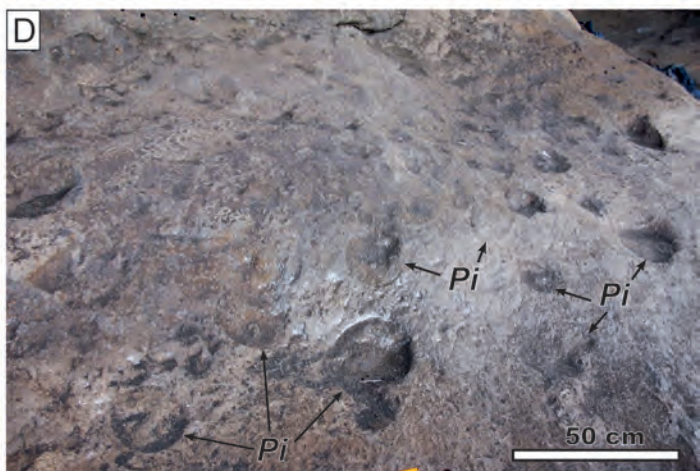
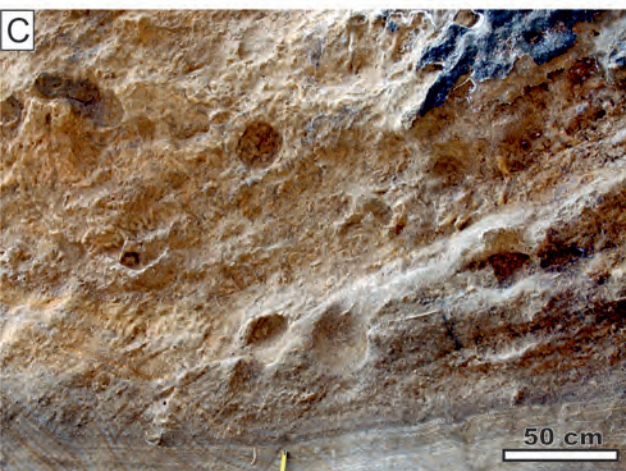
925 Costa. **A)** General view of the hole. **B)** Detailed view of the hole with imprint of snout (s) and
926 tail (t).

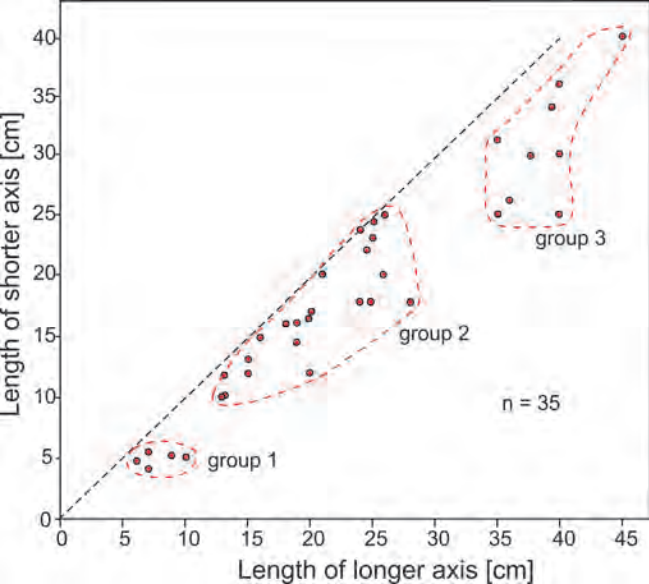
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928 FIG. 8.—Modern ray holes (incipient *Piscichnus*) and a fossil example in F. **A, B)** Ray hole on
929 a sandy tidal flat, Isla Cononados, Baja California Sur (USA); A – oblique view showing a
930 sediment carpet resulted from excavation of sand by ray; B – view from above, well-marked
931 tail part with rill marks resulting from channelized water flow. **C–E)** Eagle ray holes from an
932 estuary tidal flat, Whatangeau Estuary, Northern Island (New Zealand); C – the small pools
933 on the sediment's surface are ray holes; D – a fresh eagle ray hole with outlined shape of ray
934 body and the deepest part excavated by water jet from mouth; E – shell hash of the bivalve
935 *Macomona* from faeces of the ray; two valves of *Macomona liliana* to the right. **F)** *Piscichnus*
936 *waitemata* in vertical cross section in its type locality, Miocene sandstones of the Cape
937 Rodney Formation, Waitemata Group, Mathesons Bay, Northern Island (New Zealand).

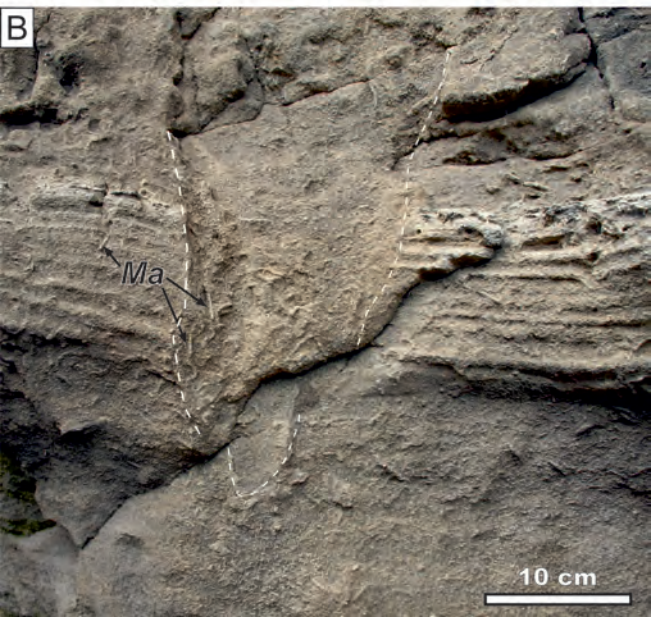
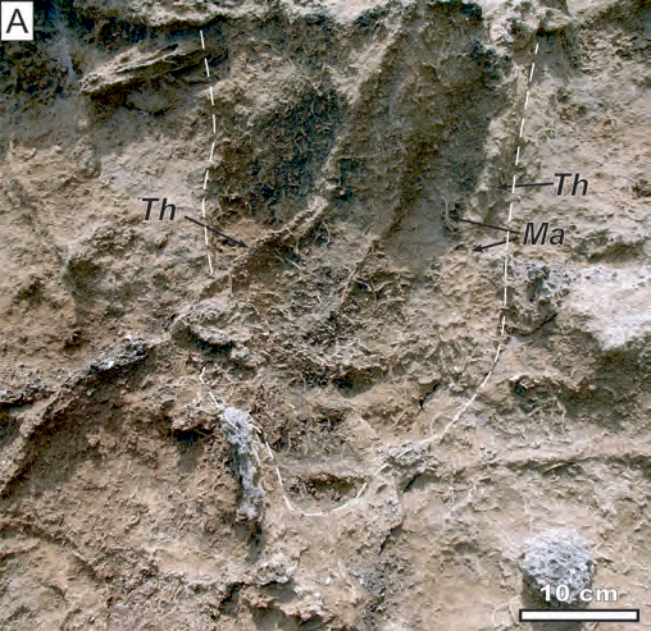
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939 FIG. 9.—Model of *Piscichnus waitemata* in trace fossil assemblage and its abundance in the
940 Pliocene sediments of Santa Maria guyot (Azores). **A)** Tier model of the basic trace fossils.
941 The schematic drawings not to the scale. **B)** Abundance of *Piscichnus* in relation to
942 controlling factors in the Pliocene sediments deposited on top of the guyot/shallow bank of
943 Santa Maria.

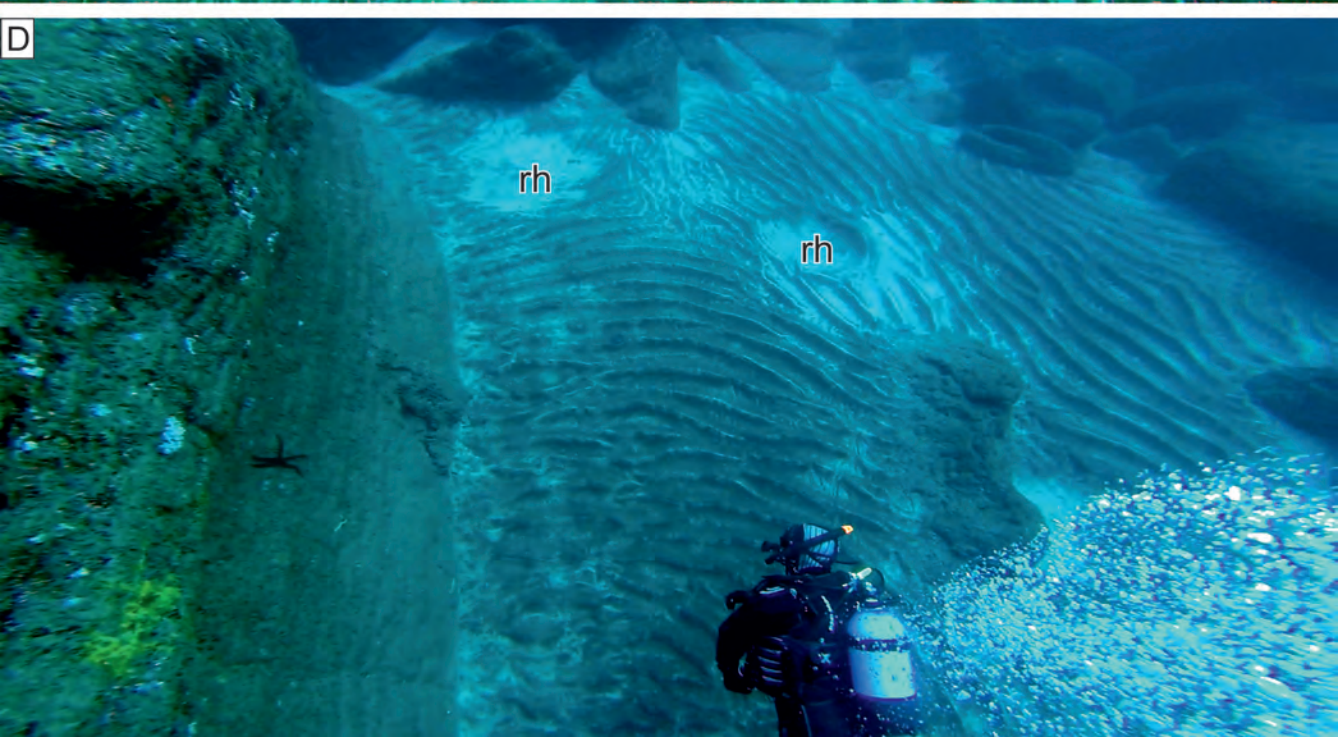


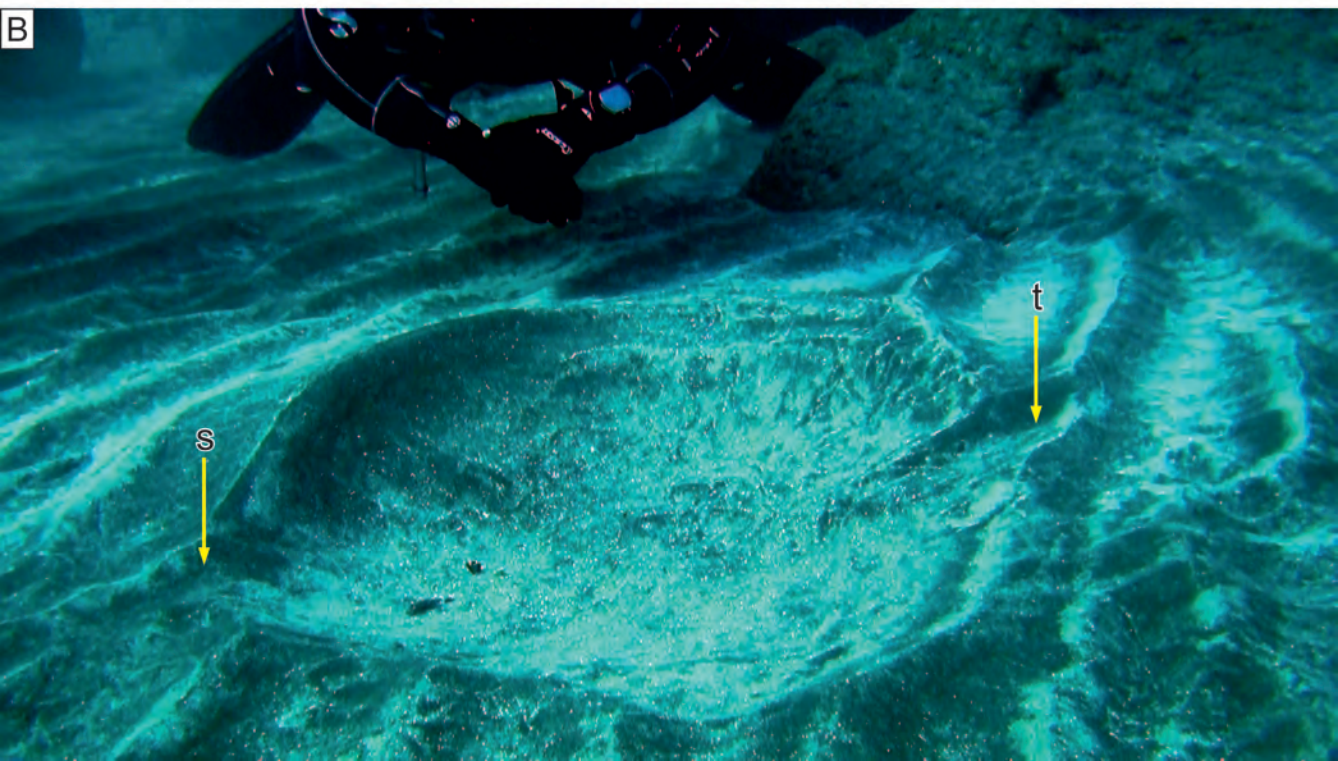






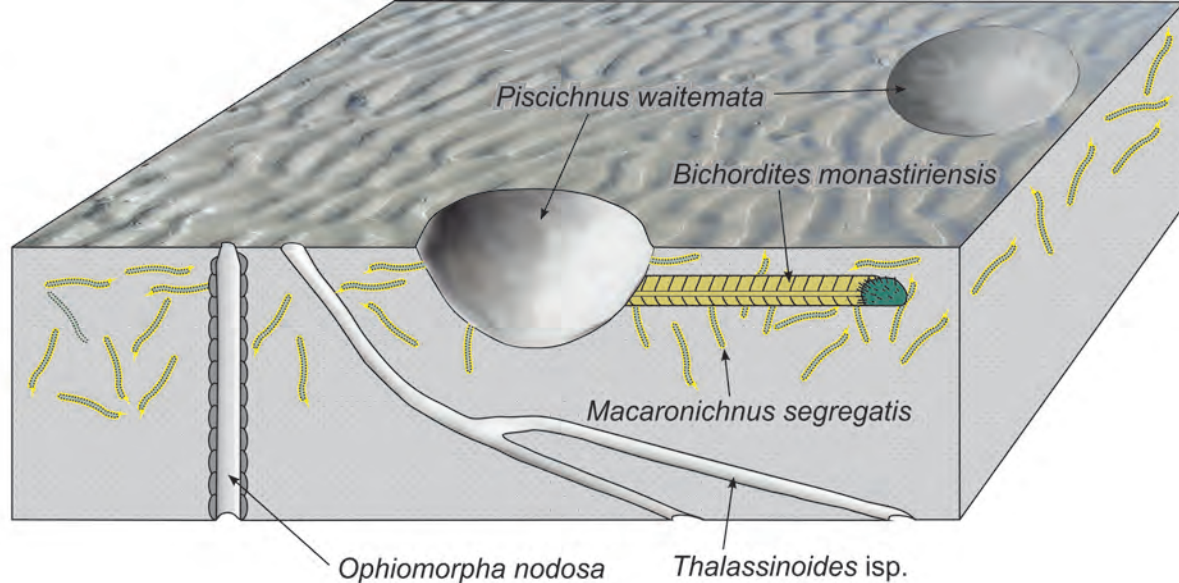




A**B**



A



B

